AUTOTOMY IN HOLOTHURIANS.[1]

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I. Introduction.

It seems remarkable that any animal should make a regular practice of casting off parts of its body, and it is not strange that autotomy has long been a subject of more than passing interest to the scientific world. Although this phenomenon is present in a variety of animals it has been most fully studied in the arthropods and echinoderms. In the first of these groups the nervous control of the reflexes concerned has been investigated (Drzewina, :07; Morgan, :02), and there seems to be no doubt that autotomy may occur as a result of stimulation which exerts no direct mechanical strain on the parts thrown off (Torre Bueno, :08). It is even maintained to be a psychic phenomenon in some cases (Pieron, :07) which is due to conditions within the animal itself. Many echinoderms are known to break off portions of the body as a result of external stimulation (Lang, '96), but, to my knowledge, no studies directly concerned with the nervous control of such reactions have been made.

The experiments described in this paper were performed upon the two common holothurians which are found at Woods Hole, *Leptosynapta inhærens* (O. F. Müller) and *Thyone briareus* (Leseur). The object of the work was to discover the relationship of the central nervous system to the reflexes involved in autotomy. Evidence was obtained in two different ways. In one method of experiment various chemicals were injected into the body cavity, and their effect upon the general behavior of the animal was observed in connection with the phenomenon of self-mutilation. In another series of experiments animals were cut in two and the subsequent reactions of the two ends were compared. In this way evidence as to the importance of the nerve ring was obtained.

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II. Mechanism of Autotomy.

As Lukas (: 05) has pointed out the place where self-mutilation takes place is usually determined definitely by the structure of an animal, and in the two genera under consideration the process is quite different. *Leptosynapta* constricts off pieces at the posterior end of the body (Fig. 1) until there is often only a small anterior fragment remaining. Such fragmentation is brought about by the strong local contraction of the circular muscles which pinch the body in two.

Thyone never constricts off pieces at the posterior end. In autotomy the body-wall breaks open just behind the calcareous

Fig. 1. *Leptosynapta inhærens*, showing method of autotomy.

ring, at the point indicated by *b* in Fig. 2, and the visceral organs are thrown out. If the body is in the position shown in the figure, however, there will be no autotomy for the contraction of the circular muscles at *c* forces the calcareous ring (*c.os.*) back into the body. But if the tentacles are extended and the calcareous ring is pushed forward a break may occur at *b*, as a result of the strong contraction of the circular muscles at that point, and visceral organs are forced out. The calcareous, water-vascular and nerve rings are thus ejected from the body, together with the tentacles (*t*) and more or less of the alimentary canal (*s*, *i*). Whether this autotomy takes place or not depends upon the breaking of the inner branch (*l.m.2*) of the longitudinal muscle bands (*l.m.*), whose normal function is to retract the calcareous ring (*c.os.*). When the strain brought about by the contraction of the circular muscles (*c.m.*) becomes too great these inner bands are torn asunder, usually at the point *x*.

III. Dependence of Autotomy on the Presence of the Anterior Portion of the Body.

In *Leptosynapta* (Fig. 1) the manner of the fragmentation of the body points to an influence which perhaps comes from the circumoral nerve ring. Pieces are always constricted off from the body at the posterior end and fragments thus separated do

not again break up, as is the case in the arms of some ophuroids. Furthermore, if an individual is cut in two in the middle of the body the posterior half does not constrict off pieces, though it undergoes irregular contractions and constricted rings are often formed. The anterior half however will continue to fragment at its posterior end. The results are the same if an animal is cut in two in such a way that the posterior piece contains two thirds or three fourths of the body.

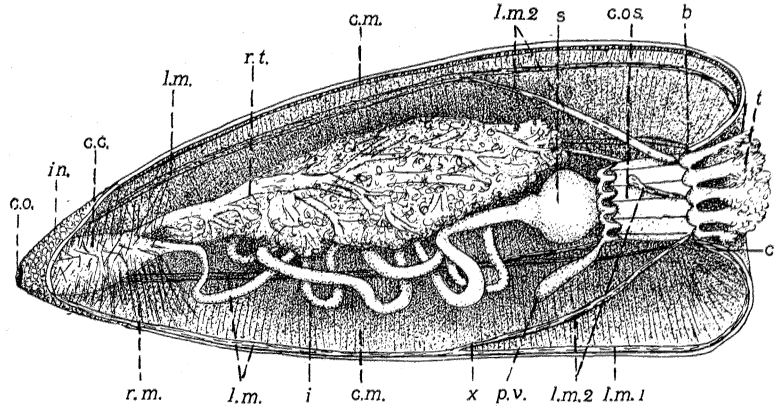

FIG. 2. *Thyone briareus*. The right side of the body-wall as well as some of the dorsal portion have been removed. The ampullæ and mesenteries are not shown. *b*, point where body wall is ruptured in autotomy ; *c*, region where circular muscles are effective in preventing autotomy ; *c.c.*, cloacal chamber ; *c.m.*, circular muscles ; *c.o.*, cloacal opening ; *c.os.*, calcareous ring ; *i*, intestine ; *in.*, integument ; *l.m.*, longitudinal muscle bands ; *l m.1*, outer branch of longitudinal muscle bands ; *l.m.2*, inner branch of longitudinal muscle bands ; *r.m.*, radial muscles which dilate the cloacal chamber ; *r.t.*, respiratory tree ; *s*, stomach ; *t*, tentacles ; *x*, weak point in inner branch of longitudinal muscle band.

Thyone's mutilating reflexes always involve the loss of the nerve ring and the remaining portions of the body do not undergo further fragmentation but ultimately regenerate the lost parts. As in *Leptosynapta* there is no autotomy when the portion of the body which contains the nerve ring is absent.

IV. Effect of Chemical Substances on Autotomy.

In order to ascertain whether substances which increased the general excitability would induce a corresponding increase in the number of individuals manifesting autotomy, certain drugs and

chemicals were injected into the body cavities of two hundred and forty-six holothurians. *Thyone briareus* was the only species used for these experiments, and the animals selected were of medium size, measuring from five to eight centimeters in length. As the normal reactions of this species have been described in a former paper (Pearse, : 08), they will not be considered in detail here. Twelve individuals were experimented upon at one time, and they were placed in pairs in six finger bowls which contained sea water. The substance to be tested was injected into the body cavities of ten individuals by means of a hypodermic syringe. The two remaining animals were pricked with a needle without having anything injected into them and served as a control. Observations extended over a period of twenty-four hours in each case. Experiments were started in the morning and observations were made at intervals during the same day. The condition of the animals on the following morning was also recorded.

The results of the experiments are set forth in Table I. A volume of distilled water which exceeded that of any of the other substances used was injected into ten individuals and they were apparently unaffected by it. It was therefore assumed that the effects obtained in the other experiments were due to the specific substances which were injected.

Substances like acetic acid and clove oil, which were apparently highly irritating and caused the most intense contractions of the muscles of the body-wall, did not bring about the ejection of the visceral organs. Nor were drugs like codene and atropine, which caused violent peristaltic waves of contraction to pass over the body, any more potent in inducing autotomy. The same may be said of sodium chloride, atropine and clove oil, although the injection of any of these substances was often followed by a waving of the oral tentacles to perform "feeding" movements, thus bringing about favorable anatomical relations for autotomy. All the reactions induced by the substances mentioned indicated violent stimulation or great bodily activity, but none of them produced any increased manifestation of self-mutilation.

The injection of strychnine was followed by the largest percentage (35) of cases of autotomy and methylene blue came next (22 per cent.). Strychnine apparently caused a great increase in

TABLE I.

SHOWING THE EFFECTS OF INJECTING CERTAIN SUBSTANCES INTO THE BODY CAVITY OF *Thyone briareus* (Leseur).

	Strength of Solution.	Amount Injected in c.c.	Number of Individuals Used.	Ejected Viscera.	Violent Peristaltic Contraction Waves.	No Peristaltic Waves.	Tentacles Extended.	Body Wall Puckered from Contractions.	Very Active.	Stopped Respiratory Movements.	"Normal" after 24 Hours.	No Response to Pricking with Pin.	Died.
Acetic acid	10 %	.1–.25	20			20		20		20			20
Alcohol, ethyl	95 %	.77–3.85	10								2		6
Atropine	?	?	10		10		5[1]				10		
Chloretone	Sat. sol.	.77–3.85	10	2			2[1]				8	4	2
Chloroform	Conc.	.77–3.85	10					10		10		10	10
Codene sulphate	1 %	1–2	10	1	10		5[1]	10	10		9	4	
Clove oil	Conc.	.1–2	20			10	11[1]	6				20	20
Curare	Powder	?	20								20		
Ether	Conc.	.77–3.85	10	1		10				5		5	10
Magnesium chloride	20 %	.77–3.85	10								6	4	
Magnesium sulphate	20 %	.77–3.85	10			6					4	6	
Methylene blue	2 %	.77–1.54	18	4		18	1[1]			18			18
Morphine sulphate	1 %	.5	10								10		
Nicotine	.05 %	.15–3.85	20	2		20				8	9		11
Sodium chloride	10 %	1.55	10				5[1]				10		
Strychnine	Powder	?	20	7			1[1]		20				
Sugar	50 %	.77–3.85	9				1[1]				7	2	
Turpentine	Conc.	.77	10	2			2[1]				10		
Water, distilled	Conc.	5	9								9		
Total			246	19	20	84	33	46	30	61	114	55	97

the general activity without causing the reactions to become abnormal. The tube-feet over the whole body were waved actively back and forth, and both the peristaltic contractions of the body-wall and the respiratory movements were strong and frequent. Methylene blue, on the other hand, caused a complete cessation of such normal activities as respiratory movements and peristaltic waves; the body-wall and tube-feet were strongly contracted. This substance caused death in every instance.

Autotomy took place under quite diverse conditions in the two cases and cannot, in the light of these experiments, be affirmed to result from either "over" stimulation or extraordinary activity alone. In my opinion it may better be ascribed to what we may call a "structural accident," and it may occur when any combi-

[1] From June 22 to July 5, 1909, many individuals were ejecting eggs or sperms from the genital papilla. During this process the tentacles were extended and these reactions in the table may have been due to the physiological condition of the individuals rather than the effects of the substances injected.

nation of conditions causes the inner branches of the longitudinal muscles to be broken.

V. General Considerations.

It is apparent from the experiments which have been described that autotomy is not the result of any single factor which can be easily controlled, at least in the two species of holothurians studied. It is of more uniform occurrence in *Leptosynapta* than in *Thyone*, a fact doubtless due largely to the structural differences between them. Clark (:01, p. 25) in speaking of *Leptosynapta* says, "Autotomy is not normal or defensive, but is due entirely to pathological conditions." Some holothurians (*e. g.*, *Cucumaria*), however, are said to multiply regularly by constricting the body in two in the middle (Lang, '96). Self-mutilation probably occurs in nature as a result of such conditions as foul water or two high temperature. The process might be beneficial to either of the two species under consideration when the environmental conditions were unfavorable for existence. By throwing off a portion of the body the total amount of metabolism necessary would be decreased. An individual might thus survive until conditions were again favorable and the lost parts could then be regenerated.

It can be affirmed that autotomy is apt to occur as a result of unfavorable stimulation in both *Leptosynapta* and *Thyone*. In the former genus it is induced uniformly and regularly when the proper conditions arise, *e. g.*, lack of sand for burrowing, foul water. It might in this case be considered to be a definite reflex and evidence has been given (II., p. 43) which lends some support to such a view. The fact that the constrictions which pinch the body in two are formed only when a region is connected with the anterior portion of an animal shows that some influence which comes from the anterior end is essential. It seems reasonable to suppose that such an influence comes from the only central nervous system which holothurians possess — the nerve ring. Autotomy apparently involves a reflex in this case which is similar to those found in arthropods (Drzewina, :07; Morgan, :02; Torre Bueno, :08).

When we turn to *Thyone*, however, autotomy is by no means

so uniform and regular in its occurrence. Under the best of conditions it appears in only 35 per cent. of the possible cases. As has been stated, the phenomenon depends in this genus upon the breaking of certain muscles and the rupture of the body-wall. In some individuals there seems to be an actual struggle between the different parts of the body, and the observer is often in doubt for a time whether the longitudinal muscles will pull the visceral organs back within the body or whether the intense contraction of the general body muscles will eject them. One is easily led to believe that the activities of different parts are not well correlated, and that the part which gets the initial advantage gains control.

As the mechanism for ridding the body of certain parts is quite different in the two genera under consideration, it is not possible to compare them directly. The process is more stereotyped in *Leptosynapta*. In the opinion of the writer, the words which were just quoted (p. 47) from Clark (:01) in regard to that genus could better be applied to *Thyone* and it seems improbable that autotomy is an important factor in the daily life of the members of either genus. Nevertheless, it is easy to conceive that a process of this kind, which first arose as a result of certain structural and physiological peculiarities, might in time give rise to a process which would become advantageous to the species. In fact, this condition of affairs seems to have come about in some holothurians (*e. g.*, *Cucumaria*) which multiply by constricting the body in two in the middle.

The tendency toward autotomy is apparently marked in the holothurian line. It is a phenomenon which is accompanied by remarkable powers of regeneration and in some species it has become a beneficial process, but in others it is comparatively unimportant, if not actually harmful.

VI. Summary.

1. In *Leptosynapta inhærens* autotomy occurs regularly when unfavorable conditions of environment arise. Experiments with *Thyone briareus* did not show more than 35 per cent. of cases of autotomy, even under the most favorable circumstances for its occurrence.

2. The mechanism involved in autotomy is quite different in the two genera. *Thyone* breaks the longitudinal muscles and throws out the visceral organs at the anterior end. *Leptosynapta* constricts off pieces at the posterior end of the body.

3. Portions of the body which have been separated from the anterior region, which contains the nerve ring, do not show autotomy.

4. Strong stimuli which bring about a very active or a strongly contracted condition do not always induce autotomy.

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